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THE INHERITANCE OF THE WEAK AWN IN CERTAIN AVENA CROSSES¹

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(In cooperation with the Office of Cereal Investigations, U. S. Department of Agriculture.)

FOR some time past, the writers have had under observation many different hybrid series of oats. Certain of these offer an excellent opportunity for a study of the inheritance of awns. This paper is a preliminary report aiming to set forth ideas regarding the factor differences between certain types of awns, as a basis for a further study of the relation between awning and other characters of the oat grain.

KINDS OF AWNS

Practically all of the wild types of oats are characterized by a very strong awn. This awn is typically long, stiff, and geniculate. The basal portion of the strong awn is twisted in a clockwise fashion and either black or dark brown in color. Above the twist, the awn is practically straight until it reaches the knee, at which point it turns sharply and proceeds almost at right angles to its former course and usually in a different plane. The first step in the modification of this type of awn seems to be the loss of geniculation, together with a reduction of the stiffness. Then a further straightening of the awn occurs, leaving it practically straight from the point of attachment to the tip. Such a change is accompanied by a loss of the dark color at the base of the awn. An awn of this last type is usually spoken of as the *weak awn*. The weak awn may vary greatly in length, thickness, and rigidity. In some cases it becomes a mere hair-like appendage,

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FIG. 1. Showing gradations between the spikelet possessing two strong awns, and the awnless spikelet. From left to right are shown: 2 strong awns; 1 strong and 1 weak awn; 1 strong awn; 2 weak awns; 1 weak awn; and the awnless type.

extending scarcely beyond the tip of the lemma and only distinguishable by careful examination. As this awn becomes weaker, it is produced nearer to the tip of the kernel; that is, the rib of the lemma which forms the awn adheres to the lemma for a greater distance before arising as an awn. Among the wild and cultivated types of oats the awns are either characteristically strong, weak, or lacking altogether. In hybrids of these, however, the awns may present all gradations between the awnless and the very strongly awned types. It is usually possible, though, to classify the hybrids as having strong, intermediate, or weak awns. (See Figures I and II.)

METHODS OF STUDY

The parent plants and first-generation hybrids were grown in the greenhouse, and the second and third generation hybrids were grown in the field. In the case of the first-generation hybrids, all of the spikelets on all of the plants could be studied. With the much larger F_2 , however, it was found impracticable to attempt to study all of the spikelets on a plant. The study was limited,



FIG. 2. Showing gradations in the weak-awn series, from a spikelet having two weak awns down to the awnless type.

therefore, to one representative panicle from each plant. The spikelets were picked from such a panicle, examined for awns, and placed in a small seed envelope on which was recorded the data as to total number of spikelets, number with one awn, and number with two awns.

MATERIAL

The weak-awned varieties reported on here are the Burt and a strain of the Red Texas. Attention was centered upon the variety Burt. The awnless type in all cases was the cultivated variety Sixty-Day. For the strong-awned oat, a strain of *Avena fatua* was used. All forms had been grown in pure line culture previous to crossing and were uniform within themselves.

Series 514a1 — Burt \times Sixty-Day (Weak Awn \times Awnless)

A cross between the Burt and Sixty-Day gave an F_1 which was almost awnless. A few plants had awns on some of the spikelets, but the generation could be considered practically awnless.

The second generation plants showed all degrees of awning, from the perfectly awnless condition to those which were one hundred per cent. awned like the Burt parent. These F_2 individuals were first grouped according to percentage of awned spikelets, with a class range of ten per cent. (Table I.)

TABLE I
 F_2 OF 514A1²

Per Cent. of Awning	<i>t</i>
0	110
1-10	29
11-20	23
21-30	25
31-40	18
41-50	18
51-60	14
61-70	8
71-80	12
81-90	5
91-99	12
100	66

The occurrence of plants having varying percentages of awned spikelets and forming a more or less continuous series between the parental types, at first suggested a multiple factor condition for awning. A study of the frequencies, however, showed that such an assumption was incorrect. The frequencies of the zero and 100 per cent. classes were too high to accord with an hypothesis of this sort.

When the F_2 plants were grouped in the classes—awnless, partially awned, and fully awned, it was seen that the data approached, in a general way, a ratio of 1:2:1. (See Table II.) The ratio of the first two named classes to the third was found to be 4.15:1, or, on a basis of four, 3.22:.78.

It remained for a study of the F_3 material, however, to throw light upon the number of factors concerned in this cross, and the relation of these factors to each other.

² It was necessary to reduce the class range in the case of the 91-99 class, in order to provide the 100 per cent. class. This, however, could have no effect on the conclusions drawn from this table.

TABLE II

 F_2 OF 514A1

Awnless	110	274
Partially awned	164	
Fully awned	66	
	340	340

Behavior of the Fully-awned F_2 Plants.—Seed of three of the fully-awned F_2 plants was sown in pedigree culture for an F_3 . The results obtained are shown in Table III.

TABLE III

 F_3 FROM FULLY AWNED F_2 PLANTS—514A1

Pedigree	% Awns in F_2	Awnless	Partially Awned	Fully Awned
514a1-22	100	0	0	47
514a1-88	100	0	0	36
514a1-95	100	0	0	20
Total	...	0	0	103

From this data, it would appear that the fully-awned type is the pure recessive. We have already seen that this type has very little influence on the F_1 hybrid, and that it appears in F_2 in only about 25 per cent. of the individuals. Here we find the fully-awned plants breeding true.

Behavior of the Partially-awned F_2 Plants.—Twelve plants which showed some awning in the second generation were planted in pedigree rows for F_3 . The percentage of awning in these plants varied from eleven to eighty-seven. In spite of the wide difference as to percentage of awning, their behavior was strikingly similar. With but one or two exceptions, the ratio of plants not fully awned to those which were fully awned was close to 3:1. A total of all these F_3 plants gave the frequencies 419:118, or a ratio of 3.12:88. In this case the deviation is 2.4 times as great as the probable error, but this can be accounted for by the somewhat wide deviations occurring in cultures 106 and 194. With the exception of these pedigrees, the deviations from the expectancy are not more than twice the probable error. It is of

interest to note that plants with a high percentage of awned spikelets in F_2 did not tend to give a correspondingly high number of awned plants in F_3 . Neither did plants with a low percentage of awns in F_2 tend to produce more of the awnless or partially-awned types in F_3 .

TABLE IV
 F_3 FROM PARTIALLY AWNED F_2 PLANTS—514A1

Pedigree	Per Cent. Awns in F_2	Awnless	Partially Awned	Fully Awned	Not Fully Awned	Fully Awned	Ratio $\times 4$	D	P.E.	D/P.E.
514a1- 55	77	13	16	11	29	11	2.90 1.10	.10	.185	.54
-100	24	36	17	19	53	19	2.94 1.06	.06	.137	.44
-106	11	31	7	5	38	5	3.54 .46	.54	.178	3.03
-119	20	17	8	11	25	11	2.78 1.22	.22	.195	1.13
-128	87	24	11	12	35	12	2.98 1.02	.02	.171	.12
-138	32	13	15	5	28	5	3.39 .61	.39	.203	1.92
-172	15	26	6	8	32	8	3.20 .80	.20	.185	1.08
-194	14	36	19	11	55	11	3.33 .67	.33	.144	2.29
-200	18	24	12	11	36	11	3.06 .94	.06	.171	.35
-216	30	11	18	8	29	8	3.13 .87	.13	.192	.67
-244	60	13	17	7	30	7	3.24 .76	.24	.192	1.24
-264	81	23	6	10	29	10	2.97 1.03	.03	.187	.16
		267	152	118	419	118	3.12 .88	.12	.05	2.40

Behavior of the Awnless F_2 Plants.—Eleven of the awnless F_2 plants were selected for study in F_3 , and seed from them was sown in short pedigree rows. The behavior of these plants is shown in Table V. Five of these awnless plants bred true to the awnless condition, giving a total of 249 awnless plants in F_3 . The other six broke up into awnless, partially-awned, and fully-awned plants. In no case did the ratio of these types suggest a 1:2:1 ratio. When we group all of the plants which are not one hundred per cent. awned, however, and compare them

with the fully-awned plants, we find that the separate ratios closely approximate a 3:1 ratio. The ratio for all six plants is 2.97:1.03, and its deviation is practically the same as its probable error.

TABLE V
 F_3 FROM AWNLSS F_2 PLANTS—514a1

Pedigree	Per Cent. Awns in F_2	Awnless	Partially Awned	Fully Awned	Not Fully Awned	Fully Awned	Ratio $\times 4$	D	P.E.	D/P.E.
514a1-34	0	48	0	0	48	0				
-126	0	75	0	0	75	0				
-185	0	31	0	0	31	0				
-336	0	32	0	0	32	0				
-232	0	63	0	0	63	0				
Total	..	249	249	..				
514a1-339	0	34	0	8	34	8	3.24 .76	.24	.180	1.33
-36	0	52	3	15	55	15	3.14 .86	.14	.140	1.00
-176	0	26	6	11	32	11	2.98 1.02	.02	.178	.11
-221	0	11	4	7	15	7	2.73 1.27	.27	.249	1.08
-247	0	18	7	15	25	15	2.5 1.5	.5	.185	2.70
-291	0	29	3	11	32	11	2.98 1.02	.02	.178	.11
Total	..	170	23	67	193	67	2.97 1.03	.03	.072	.43

It is apparent from these data that the F_2 grouping used here includes in the awnless class certain individuals which are heterozygous for awning, and which really belong with the partially-awned plants. According to Nilsson-Ehle (1914) environmental conditions have an effect upon the production of awns. It is quite possible that the failure of these six plants to produce some awns is due to undetermined environmental factors.

A comparison of the relative numbers of awnless and partially-awned plants in Tables IV and V would seem to indicate that awnless F_2 plants tend to give a higher percentage of awnless plants in F_3 than do the partially-awned plants. This may be explained, however, by the

fact that a high percentage of the awnless plants in the second generation were yellow in color and consequently many of them might well carry a factor which inhibits awn formation. Data will later be presented to show a definite linkage between the awn-inhibiting factor and the factor for yellow color in the Sixty-Day.

Series 2501a1 — Burt \times Sixty-Day

A second series of hybrids between Burt and Sixty-Day behaved in a manner similar to series 514a1. The F_1 was nearly awnless in both the direct and reciprocal crosses. The F_2 results are shown in Table VI.

TABLE VI

F_2 OF 2501

Pedigree	Awnless	Partially Awned	Fully Awned	Not Fully Awned	Fully Awned	Ratio $\times 4$	D	P.E.	D/P.E.
2501b1	26	96	43	122	43	2.96 1.04	.04	.0909	.44
2501ar1	17	61	28	78	28	2.94 1.06	.06	.1134	.53
2501ar2	4	32	17	36	17	2.72 1.28	.28	.1604	1.75
2501ar3	1	11	4	12	4	3.00 1.00	.00	.2921	0.00
Total	48	200	92	248	92	2.92 1.08	.08	.0634	1.26

2501b1 = Burt \times Sixty-Day.

2501ar1 = Sixty-Day \times Burt—selection of partially awned F_1 plants.

2501ar2 = Sixty-Day \times Burt—selection of awnless F_1 plants.

2501ar3 = Sixty-Day \times Burt—unselected F_1 .

It will be seen from Table VI that the partially-awned and awnless types of F_1 gave practically the same behavior, each throwing about 25 per cent. of fully-awned plants in F_2 .

Series 2401a1 — Red Texas \times Sixty-Day

A cross between Red Texas (weakly awned) and Sixty-Day gave an F_1 showing only 1.3 per cent. of awning. The second generation of this cross has not yet been grown.

Discussion of Results in Weak-awn \times Awnless.—From the data presented above, the following conclusions may be drawn as to the inheritance of awns in crosses between the weak-awned and the awnless types of oats.

The awnless type is almost completely dominant in the first generation, only a few of the plants possessing awns and those in small percentages.

The second generation gives awnless, partially-awned and fully-awned plants in a ratio which approximates 1:2:1. The totals of data from second generation plants of series 2,501 and 514 are reasonably close to this ratio:

	Awnless	Partially Awned	Fully Awned
Series 2501.....	110	164	66
Series 514.....	48	200	92
Total.....	158	364	158
Expectancy.....	170	340	170

The behavior of the fully-awned plants shows that this type is the pure recessive, for it breeds true in all cases from the second generation.

All of the partially-awned F_2 plants proved to be heterozygous, throwing in the third generation approximately three plants not fully awned to one fully-awned plant.

The awnless plants of the second generation were found to comprise both homozygous plants of the parental type and heterozygous intermediates which later broke up in the same manner as the partially-awned F_2 plants. It might be expected that some of the awnless F_2 plants would prove to be heterozygous, since awnless plants are found commonly in the first generation.

From these results, it is apparent that we cannot correctly speak of the awnless oat as the dominant type, nor should we restrict the use of the term intermediates to those plants which are partially awned.

It seems very probable that the difference between the weak-awned and the awnless varieties of oats, at least in the varieties studied, may be accounted for by the assumption

tion of a difference in one pair of genetic factors. It may be that awnlessness is a definite character which is a true allelomorph of the fully-awned condition. Some might prefer, however, to consider awnlessness simply as the absence of awning. In that case we must assume the presence of an inhibitory factor to account for the partial dominance of the awnless Sixty-Day over the weak-awned Burt. The data at hand seem to point to the presence of an inhibitor to awning in the variety Sixty-Day. A preponderance of awnless yellows in F_2 and F_3 suggests a linkage of this inhibitory factor with the factor for yellow color in the Sixty-Day. (See Table VII.) Such a finding would be in agreement with the results of Nilsson-Ehle (1914). A very definite linkage of the inhibitory factor with the factor for yellow color has already been observed in a cross between *A. fatua* and *A. sativa* var. Sixty-Day. This will be brought out in a later publication.

TABLE VII

SHOWING THE DISTRIBUTION OF REDS AND YELLOWS IN SERIES 514, WITH
PERCENTAGE OF AWNING AS RELATIVE³

	0	5	15	25	35	45	55	65	75	85	95	100
Red....	49	12	10	12	12	8	10	5	8	5	7	38
Yellow....	50	15	12	12	4	10	4	2	2	0	4	21

Certain other crosses with the Burt show that this variety contains a factor for yellow which does not inhibit awning. In the crosses Burt (red) \times Swedish Select (white), and Burt \times Early Champion (white), the F_2 contained a certain number of yellow-seeded plants, which in turn gave some yellows in F_3 . All of these yellows were fully awned. The existence of this yellow factor in the variety Burt has complicated the study of the yellow of the Sixty-Day in these crosses. The fact of the presence of this yellow in the variety Burt should be kept in mind when Table VII is examined.

It will be seen in Table VII, that the red grains are nearly as numerous in the 100 per cent. class as in the

³ The classes are as follows: -0, 1-10, 11-20, ..., 91-99, -100.

awnless class, and that the other classes are represented in practically equal numbers. In the case of the yellows, however, there are about two and one half times as many in the awnless class as in the fully-awned class. Fifty-seven per cent. of the yellows have less than 20 per cent. of awning, and seventy-three per cent. have less than 30 per cent. of awning. Many of the yellows in the 100 per cent. class are doubtless due to the yellow factor contained in the Burt parent. This factor does not inhibit awning.

Strong Awn \times *Awnless*.—The results of crosses between *Avena fatua* and the variety Sixty-Day (*A. sativa*) agree closely with those obtained in the crosses between the weak-awned and awnless types. (See Tables VIII and IX.)

TABLE VIII
F₂, TOTAL OF SERIES 2516

Pedigree	Awnless	Partly Awned	Fully Awned	Not Fully Awned	Fully Awned	Ratio $\times 4$	D	P.E.	D/P.E.
2516	169	377	201	546	201	2.92 1.08	.08	.04	2.00

TABLE IX
F₃, OF HETEROZYGOUS *F₂* PLANTS

Pedigree	Awnless	Partly Awned	Fully Awned	Not Fully Awned	Fully Awned	Ratio $\times 4$	D	P.E.	D/P.E.
687a1-15	61	124	67	185	67	2.94 1.06	.06	.07	.86
687a1-5	79	53	41	132	41	3.05 .95	.05	.089	.56
687a1-1	15	55	24	70	24	2.98 1.02	.02	.12	.17

In a similar study on *A. fatua* \times *A. sativa* var. Kherson, Surface (1916) obtained results which agree closely with those presented above. The *F₁* plants were nearly intermediate, although "The majority of *F₁* spikelets show no awn whatever" (p. 265). In the second generation the following types appeared:

Awnless	133
Intermediate	215
Wild (fully awned)	112

At first Surface assumed that the awnless plants were homozygous and should, therefore, breed true. A test of these plants, however, showed that a certain number were heterozygous. Fifteen out of twenty broke up in the third generation. This might be expected from the fact that some of the heterozygous F_1 plants were awnless. The failure of these plants to produce a few awns is attributed by Surface either to an undiscovered factor affecting awning, or to an environmental influence. It seems quite probable that the variety *Kherson* may carry a factor inhibitory to awning, similar to the factor in the *Sixty-Day*.⁴

OTHER CHARACTERS OF THE GRAIN

In connection with the above studies on awning, studies were also made on the presence of basal hairs and the type of articulation of the lower kernel of the spikelet. A strong correlation was found to exist between the fully awned condition and the Burt type (similar to that of *A. sterilis*) of articulation, and also between the fully-awned condition and the presence of medium-long basal hairs such as are found on the Burt grains. When the spikelets were all awnless, the union of the lower kernel and its rachilla was generally of the type found in *Avena sativa* and the basal hairs were either short or lacking.

It is interesting to note, in the crosses between the weak-awned and awnless types, that in every case where a panicle had two awns on a spikelet, all of the spikelets on the panicle were awned. The irregular occurrence of these two-awned spikelets, and the wide variability in numbers on a panicle, makes it seem probable that there is no definite factor for the two-awned condition. It seems more likely that the occurrence of such spikelets is due to environmental influences upon the factor for complete awning.

⁴ In some localities the names *Kherson* and *Sixty-Day* are used synonymously.

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